Similarities between British and north-west European *Aricia* "subspecies"[1] (Lepidoptera: Lycaenidae)

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Abstract: The following main *Aricia* "subspecies" are referred to in this paper: *Aricia artaxerxes allous* (GEYER, 1836), *Aricia artaxerxes artaxerxes* (FABRICIUS, 1793), *Aricia agestis* ([DENIS & SCHIFFERMÜLLER], 1775), and *Aricia cramera* (ESCHSCHOLTZ, 1821). They are referred to as "subspecies" because all are capable of cross-breeding with one another. These butterflies have between 0 and 6 submarginal lunules – orange spots – on each upper wing. One puzzling aspect is that it is possible to find individuals which show the complete range of variation within one colony. In this paper data on upper forewing lunulation are presented, together with information on several other aspects: mendelism, white scales in upper forewing discal spots, phased emergence, photoperiod and climate. The main emphasis is on upper forewing lunulation and statistical checks are applied, but it is shown that points from all the above aspects reinforce one another and indicate interpenetration of "subspecies" with a broad hybrid zone between Latitude 54° and 59° N. Any "subspecies" in this zone are identified in the text, and colonies at Durham northern England and Skåne southern Sweden are shown to be hybrids. Earlier similarities noted between British and Scandinavian colonies are extended southward to northern and central Germany. Subsequent discussion covers interpenetration, variation of colonies in the hybrid zone, and the relationship of *Aricia* "subspecies" to other butterflies, including the possibility that present forms have spread from a common ancestor.

Ähnlichkeiten zwischen britischen und anderen nordwesteuropäischen *Aricia*-„Unterarten" (Lepidoptera: Lycaenidae)

Zusammenfassung: In dieser Arbeit werden die folgenden wichtigsten „Unterarten" von *Aricia* aus Nordwesteuropa behandelt: *Aricia artaxerxes allous* (GEYER, 1836), *Aricia artaxerxes artaxerxes* (FABRICIUS, 1793), *Aricia agestis* ([DENIS & SCHIFFERMÜLLER], 1775) und *Aricia cramera* (ESCHSCHOLTZ, 1821). Sie werden hier als „Unterarten" behandelt, weil sie sich offenbar untereinander fertil paaren können. Diese Schmetterlinge haben je zwischen 0 und 6 submarginale Halbmonde (orangefarbene Flecken) auf der Flügeloberseite. Auffällig ist, daß man jeweils innerhalb einer Teilpopulation Individuen fin-

[1] The term "subspecies" is used here not to denote a systematic unity or taxonomic rank (e.g., as defined by the International Code of Zoological Nomenclature), but to describe a taxon which, in my opinion, is not a full species (because the different populations are interfertile), without deciding on their status here.

den kann, die die komplette Variationsbreite zeigen. In der vorliegenden Arbeit werden die Daten der Halbmondflecke auf der Vorderflügeloberseite präsentiert, danaben Informationen über folgende weitere Aspekte gegeben: Mendelianischer Erbgang, weiße Schuppen in den Zellschlußflecken der Vorderflügekoberseite, schubweiser Falterschlupf, Photoperiodizität und Klima. Das Hauptgewicht liegt auf den orangen Flecken der Vorderflügeloberseiten; dazu werden statistische Verfahren angewendet. Insgesamt zeigen alle angeführten Punkte Hinweise auf gegenseitige Vermischung der „Unterarten" mit offenbar einer breiten Hybridzone zwischen 54° und 59° nördlicher Länge in NW-Europa. Alle „Unterarten" innerhalb dieser Zone werden identifiziert; die Kolonien von Durham in Nordengland und Skåne in Südschweden sind Hybriden. Früher durchgeführte Vergleiche zwischen britischen und skandinavischen Populationen werden ausgedehnt nach Nord- und ins südwestliche Deutschland. In der weiteren Diskussion werden die Durchmischungszonen, die Variabilität der verschiedenen Teilpopulationen in der Hybridzone und die Vergleichsbeziehungen der *Aricia*-„Unterarten" mit anderen Tagfaltern sowie ihre mögliche Ableitung von einem gemeinsamen Vorfahren behandelt.

Introduction

The generally accepted position of the taxa of *Aricia* in Britain today is from south to north (HEATH et al. 1984):

- bivoltine *agestis* from the south coast up to Derbyshire;
- univoltine colonies designated *Aricia artaxerxes salmacis* (STEPHENS, 1831) (Derbyshire and further north in England);
- univoltine *A. a. artaxerxes* in Scotland.

A query to the Biological Records Centre re the status of the univoltine Peak district colonies in Derbyshire revealed (HEATH, pers. comm. 1971) that the distribution map for *Aricia* was due to JARVIS. *A. agestis* colonies (JARVIS 1969) were described as uniformly well-lunulated compared with *A. a. salmacis* colonies at Durham where the lunulation was very variable. Checks on Peak district specimens via museum collections and photographs led to the conclusion that the Peak district race was well lunulated. If this was so, where did lunulation become less? Eventually over 3000 specimens were examined, mainly from 23 different museums with some field records and photos. Upper forewing lunulation was quantified in order to provide a positive comparison. Specimens were examined without magnification and lunules were counted, traces or more counting as one lunule. They were then classified into Cr (crassilunulata) or Pv (parvilunulata forms). These terms were used (JARVIS 1969) to describe well and poorly lunulated

butterflies respectively. Males were less well lunulated than females, so Cr males were set at 5 or 6, females at 6 lunules. It follows that Pv males have 0-4, Pv females 0-5 lunules. Numbers for any one colony/area were built up randomly mainly covering England and Scotland with some from the continent. The data were manipulated mathematically to provide a 50/50 combination of males and females which produced a CC:CP ratio – combined Cr : combined Pv. From a statistical examination a minimum ratio of 5.0 was required for *A. agestis* and this was easily met by all bivoltine and three univoltine colonies, one of which was the Peak district (SMYLLIE 1992 a). Further north the CC:CP ratio first dipped quite distinctly below 5.0 at two colonies, one at Pickering in north Yorkshire. It was the male lunulation which had dropped – the female had not changed. Table 1 gives selected British and continental examples: it also includes subsequent data from Scandinavia and Germany.

The CC:CP ratio has the great advantage of describing the degree of lunulation of any colony by one simple figure which can then be compared with any other. The lower the ratio, the poorer the lunulation.

Table 1: Lunulation comparison between selected areas. Abbreviations: ♂ male; ♀ female; Cr crassilunulata, Pv parvilunulata; T total; CC combined crassilunulata, CP combined parvilunulata; S south; SW south west; N north; C central.

Area	♂ Cr	♂ Pv	♂ T	♀ Cr	♀ Pv	♀ T	CC	CP	CC:CP
1 Sandhammaren to 10/8	8	38	46	17	11	28	21.9	34.1	0.64
2 Skåne ex Sandhammaren	10	10	20	12	3	15	19.5	10.5	1.86
3 S England	232	49	281	184	11	195	345.0	45.0	7.67
4 Peak district	71	16	87	42	0	42	76.3	7.7	9.91
5 Pickering	18	28	44	14	0	14	19.7	8.3	2.37
6 Durham coast	10	75	85	39	23	62	46.3	77.7	0.60
7 Inland Durham	16	13	29	28	11	39	36.8	21.2	1.74
8 Solway SW Scotland	7	28	35	8	7	15	10.3	19.7	0.52
9 Perthshire C Scotland	2	115	117	13	42	55	13.9	96.1	0.14
10 Rügen N Germany	9	16	25	20	3	23	28.3	17.7	1.60
11 Mainzer Sand	10	2	12	6	0	6	11.0	1.0	11.00
12 Continental *A. agestis*	39	11	50	52	1	53	88.1	11.9	7.41
13 Continental *A. a. allous*	1	80	81	1	40	41	1.5	80.5	0.02

Scandinavian data

A substantial paper (HØEGH-GULDBERG 1966) includes data on lunulation from several colonies in Scandinavia. Some could be converted to give CC:CP ratios in Table 1, but most required more manipulation to give a comparison for both males and females which had 4-6 upper forewing lunules. This was expressed as a percentage of the total (SMYLLIE 1995), and Table 2 again compares selected colonies. There are slight modifications from that originally published plus the German data. The map in Fig. 1 indicates localities either by name or number in this Table.

Latitudes are included so that sites in different countries can be compared easily. Also the number of specimens from which the male and female percentages have been obtained are shown. Higher figures will be more stable. Both male and female percentages are given to the nearest whole number; the combined % column gives the average, i.e. a 50/50 contribution of ♂♂ and ♀♀. The right-hand classification column shows one of 3 categories. It is easiest to start with *agestis*, and here all male figures are

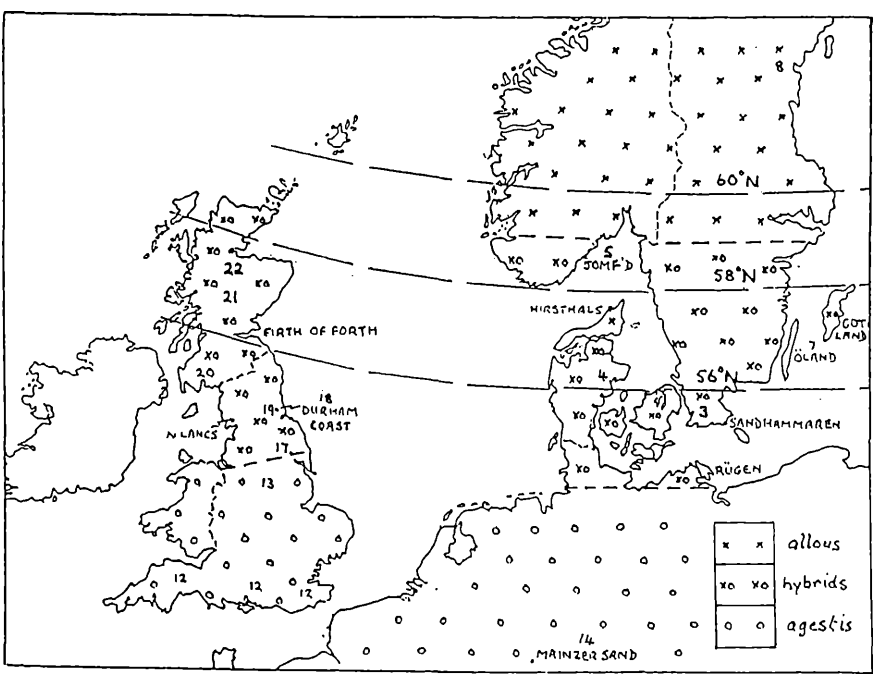

Fig. 1: Map of the location of sites in Table 2 by name or number.

96 % or more. These are significantly higher than for any other colonies and females in *agestis* colonies are all 100 % giving a combined figure of 98 % minimum. Intermediates follow at 30 to 98 %. Finally *allous* colonies are less than 30 % The demarcation line between intermediates and *allous* is arbitrary and identifies a point below which lunulation is considered poor. Note that no British colonies are in 3. The table again shows a similarity between Rügen and Pickering.

Male upper forewing lunulation

Males are less well lunulated than females, and this is advantageous when comparing lunulation characteristics of different colonies. Table 3, previously unpublished, gives the complete range of male lunulation for selected colonies and is used as the basis for column charts Figs. 2 and 3. Fig. 2 also is used to provide statistical information (see next section).

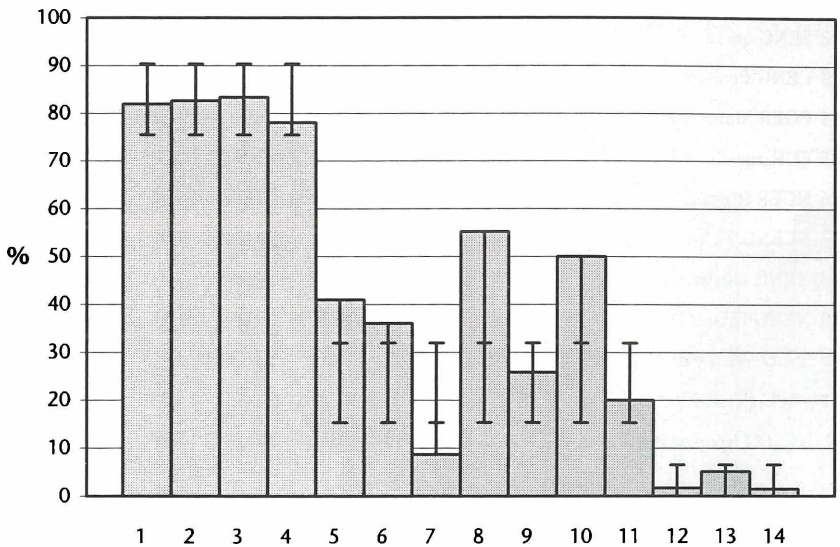

Fig. 2: Percentage of 5 & 6 lunules from Table 3 with 5 % significance limits.

Table 2: 4–6 upper forewing lunules in Britain, Scandinavia and Germany. Additional abbreviations: NC north central, DEN Denmark, SWE Sweden, NOR Norway, ENG England, EUR continental Europe, SCO Scotland; Lat. northern Latitude in ° N; L lunules; Comb. % combined percentage (as in a 50/50 contribution of ♂♂ and ♀♀); CL classification into three categories: 1 = *agestis* (98 % or more), 2 = intermediates (30–98 %), 3 = *allous* (less than 30 %).

Locality	Lat. °N	♂ 4-6 L/T	%	♀ 4-6 L/T	%	Comb. %	CL
1 Sandhammaren to 10.8	55.2	30/61	48	49/54	91	69.5	2
2 Sandhammaren 2nd brood	55.2	18/20	90	12/13	92	91.0	2
3 Skåne less Sandhammaren	55.3	44/53	83	26/26	100	91.5	2
4 DEN *agestis*	56.0	93/122	76	40/40	100	88.0	2
5 SNOR Jomfruland	59.0	6/42	14	26/29	90	52.0	2
6 SWE Gotland	57.5	7/24	29	14/14	100	64.5	2
7 SWE Öland	56.5	9/24	37	6/9	67	52.0	2
8 SWE Ångermanland	63.5	0/8	0	5/9	56	28.0	3
9 NDEN Hirsthals	57.5	5/241	2	25/96	26	14.0	3
10 NNOR Lyngenfjord	69.5	0/9	0	1/5	20	10.0	3
11 EUR *allous*	–	7/65	11	14/35	40	25.5	3
12 SENG *agestis*	51.0	214/233	96	137/137	100	98.0	1
13 CENG Peak district	53.0	85/87	98	42/42	100	99.0	1
14 CGER Mainzer Sand	50.0	12/12	100	6/6	100	100.0	1
15 EUR agestis	–	48/50	96	53/53	100	98.0	1
16 NGER Rügen	54.2	19/25	76	23/23	100	88.0	2
17 NCENG Pickering	54.2	36/44	82	14/14	100	91.0	2
18 NENG Durham coast	54.8	25/92	27	30/39	77	52.0	2
19 NENG Inland Durham	54.6	21/29	72	29/29	100	86.0	2
20 SSCO Solway district	54.9	15/35	43	13/15	87	65.0	2
21 CSCO Perthshire	57.0	16/117	14	34/55	62	38.0	2
22 NCSCO Invernesshire	57.5	11/39	28	14/19	74	51.0	2

Points to be noted from the right-hand column in Table 3 or from Fig. 2 are the high and consistent figures for 5 and 6 lunules for *agestis* colonies nos. 1-4, the low consistent figures for the northern *artaxerxes* colonies nos. 12-14, and the considerable variation in the remainder, nos. 5-11. The 0 lunules column shows the same general effect but in reverse – see Fig. 3.

Table 3: Male upper forewing lunulation for selected colonies. Abbreviations see above.

		♂♂	lunules [n]						lunules %		
		total	0	2	3	4	5	6	0	2–4	5–6
1	SENG counties	177	–	1	9	22	67	78	0.0	18.1	81.9
2	CENG Peak District	138	1	–	2	21	64	50	0.7	16.7	82.6
3	CGER Mainzer Sand	12	–	–	–	2	7	3	0.0	16.7	83.3
4	EUR *agestis*	50	–	–	2	9	18	21	0.0	22.0	78.0
5	NCENG Pickering	44	–	1	7	18	8	10	0.0	59.1	40.9
6	NGER Rügen	25	1	1	4	10	8	1	4.0	60.0	36.0
7	NENG Durham coast	172	56	26	40	25	12	3	32.6	58.7	8.7
8	NENG Durham inland	29	3	1	4	5	10	6	10.3	34.5	55.2
9	SSWE Sandhammaren	62	9		37		16		14.5	59.7	25.8
10	SSWE Skåne ex Sandh'n	20	1		9		10		5.0	45.0	50.0
11	SWSCO Solway district	35	7	2	11	8	4	3	20.0	60.0	20.0
12	CSCO Perthshire	117	72	8	21	14	2	0	61.5	36.8	1.7
13	NCSCO Invernesshire	39	20	4	4	9	1	1	51.3	43.6	5.1
14	EUR *allous*	65	37	9	12	6	1	0	56.9	41.6	1.5

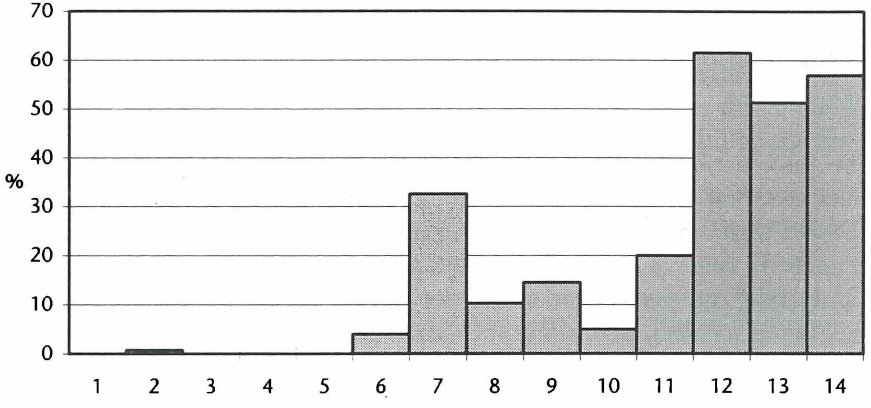

Fig. 3: Percentage of 0 lunules from Table 3.

Statistical checks

In Britain the greatest number of colonies and resulting specimens is in the south and reduces steadily further north. Museum collections contain more examples of *agestis* than other "subspecies", and it is therefore best to start with *agestis*. A statistical check on the effectiveness of lunulation data can be obtained via the formula:

$$n\,p \pm k\sqrt{p\,q\,n}$$

where n is the number of specimens in the sample, p is the proportion with a given characteristic, for example male 5 and 6 lunules, q is the remainder, and k is a constant which depends on the degree of significance selected. For 5% significance $k = 1.96$. This is the standard choice and means that limits can be drawn up for a sample of any number n, and that statistically similar groups will be within the limits: there is only a 5% chance (1 in 20) of a similar group being outside the limits. All male specimens from colonies in each of the three classes mentioned have been checked to find the average figures for their 5 and 6 lunule content, and the data are condensed into Table 4.

Table 4: Statistical comparisons for male upper forewing lunulation data.

	Total n	5&6 L	p	np (n=100)	$k\sqrt{pqn}$	High %	Low %	T3	all
agestis	850	705	0.829	82.9	7.4	90.3	75.5	4/4	21/21
hybrids	721	170	0.236	23.6	8.3	31.9	15.3	2/7	4/14
all./art.	384	12	0.031	3.1	3.4	6.5	0	3/3	8/8

The information in Table 4 needs expanding. The left-hand column 1 gives the total number of male specimens followed by 2 which gives the number with 5 and 6 upper forewing lunules. Then 3 gives p = column 2 divided by column 1. The 5 % significance limits vary with sample size, the smaller the sample the wider the limits. This is why column 4 has been set at n = 100, a constant but reasonably high figure. Column 5 gives the ± figure, producing the High and Low 5 % significance limits in columns 6 and 7. Column 8 (T3) shows the number of colonies/areas in Table 3 which are inside the limits compared with the totals, and the right-hand column 9 gives the picture for all colonies/areas for which there is data. In 9 some of the Table 3 data has been split into smaller units, e.g. individual old English counties for *agestis*. Other old counties

and the other two univoltine areas have been added. The middle column labelled hybrids is split into 1 km squares in Durham and north Lancashire. In Britain it goes from Pickering to the north of Scotland. The bottom line labelled *allous/artaxerxes* contains specimens north of 56° N in Scotland in 6 old counties groups and also includes a series of *Aricia artaxerxes vandalica* (KAABER & HØEGH-GULDBERG, 1961) from Hirsthals, north Denmark which are in JARVIS' collection at the Natural History Museum in London, plus the European *allous* figures.

The 5 % significance limits from Table 4 are shown in Fig. 2 for the 3 classes to which they relate. They show that nos. 1-4 are all well within their limits, as are nos. 12-14. The same applies to the larger picture in column 9. In these overall checks individual calculations have been made to produce 5 % significance limits for each colony/area. However, the hybrids in the intermediate zone show a very different picture, and it must be rememered that the highest and lowest figures in Durham and south Sweden are from colonies very close together. Provided any specimen had its locality labelled it was accepted. Thus the data bank takes no account of climatic variation, whether the specimen was first, second or only brood, what the foodplant was, whether it was caught in the wild or bred and if bred whether this was via normal or forced heat and light conditions. The approach is rugged enough and stable enough to produce consistent results for males. The same goes for *agestis* females where 487 out of 512 have 6 lunules giving a higher figure for p of 0.951. Some of these are in Tables 2 and 3: again when split up into old counties or identified areas all are within the 5 % significance limits. The above figures for *agestis* are impressive and provide a stable position against which to judge the lunulation of any other colony.

Returning to the bottom line, while the male lunulation is consistently low, female lunulation is much higher and variable as Table 2 shows, thus leaving all Scotland in the hybrid zone. A check on *cramera* lunulation showed that out of a total of 37 specimens, 20 males and 17 females, all had the full complement of lunules although males did show some variation in lunule size.

As far as specimens with 0 lunules are concerned, the *agestis* colonies have virtually none, while in the group with Scotland north of Lat. 56° N there is a total of 222 males out of the 384, making p = 0.578, and the median line at 57.8 %. All the colonies are within the 5 % significance limits.

The percentage of 0 lunule males will rise further in colonies in north Sweden and Norway; HØEGH-GULDBERG records that at Lyngenfjord, the most northerly colony, no males were seen with any lunules. As far as males are concerned, there may be two stable lunulation zones, one with p near 1 and another at p = 0.578. However, more work would be needed to investigate this aspect. The p = 0.578 figure is useful when looking into the constitution of colonies at Durham and Sandhammaren.

Pickering and Rügen

The first distinct drop in male lunulation compared with *agestis* occurs at Pickering in north Yorkshire which is only 18 km westnorthwest from the nearest *agestis* colony in the Yorkshire Wolds. At Pickering the 5 and 6 lunule content at 40.9 % is roughly half that of the *agestis* colonies, a large difference well outside the 5 % significance limits. At the same time the 0 lunule content has not increased, while at other colonies further west and north the 0 lunule content is significant. Pickering does therefore have characteristics which represent the start of lunulation change just outside the *agestis* limit. Since there are similarities between the colonies at Durham and south Sweden which both contain a significant 0 lunule content, it seemed worthwhile seeking a possible parallel to Pickering in north Germany. Thanks to the interest and expertise of Dr. Klaus SCHURIAN both bred and wild specimens were obtained from Inseln Rügen and their lunulation characteristics are included in the Tables.

It is difficult to be precise in any comparison, and in this case the difficulty lies in the single 0 lunule specimen shown in Table 3. Many more specimens would need to be checked to decide what the 0 lunule content finally is. In the case of the Peak district the 0 lunule specimen occurred early, but has not recurred in a total of 138. There is a distinct similarity between the lunulation patterns for Pickering and Rügen, and even if a low 0 lunule content were to be confirmed, it is still near the change from *agestis*. The lunulation approach has identified a gap in the north-south progression east of Britain in Scandinavia which has been looked for and confirmed by the presence of the colony at Rügen.

Gregor MENDEL (1822–1884)

While abbot of the monastery at Brünn in Austria (now Brno in the Czech Republic), MENDEL carried out many cross-fertilisation experiments on sweet and garden peas. The results led him to develop his particulate theory which in 1900 was accepted as the foundation of modern genetics.

His theory assumed that characteristics are passed on as particles (now known as alleles) from each parent to the offspring. Individual particles can never be eradicated; for example when a red sweet pea is crossed with a white one, although the F1 generation are all pink and all traces of the parents appear to have gone, parts of subsequent generations will revert to red and white. In fact the F2 generation will contain 25 % red, 25 % white and 50 % pink. Although simple, these figures are important. An original 50/50 ratio of white and red has been diluted in the second generation to 25/25 with the remaining 50 % being intermediates. Implications for *Aricia* are similarly important: firstly if there has been any cross-breeding between *agestis* and *artaxerxes* which have significant numbers of 6 and 0 lunule individuals respectively, then both 6 and 0 lunule specimens will occur, even if only very occasionally. Since females are better lunulated than males, it is females which will be more likely to provide examples at the 6 lunule end of the spectrum, and males at the 0 lunule end. The same principles will apply to larval shape and colour, to photoperiod reaction/rate of growth, and also where applicable to white discal spots. Secondly and of equal importance, individuals with characteristics of their parents will occur much less frequently than the parents' original %, the gap being filled with intermediates of varying characteristics in the real-life complex position of today's colonies which have developed over very long periods.

Durham and Sandhammaren in Skåne

The colonies in these two areas, one in north England and the other in south Sweden, share important similarities. Looking first at male 5 and 6 lunules, Skåne ex Sandhammaren at 50.0 % and inland Durham at 55.2 % both contain the best lunulations in their respective colonies in the 54° to 59° N zone. These colonies are near others on the coast in Durham and at Sandhammaren which are relatively poorly lunulated and which also have a higher 0 lunule content. The figures are not by any means identical but the trend is there, and the differences occur between colonies rela-

tively near one another; they are typical of colonies in the wider latitude band because there is no consistency either in the male 5 and 6 lunule or in the 0 lunule content. If the *agestis* figures mean anything, a "subspecies" should have consistent lunulation.

Taking the situation in England first, *salmacis* is said to be a "subspecies", yet it consists of univoltine colonies in its southernmost region with *agestis* lunulation, coupled with the colony at Pickering which has a very low 0 lunule content, with the more typical variable colonies centred on Durham where both 0 and 5 to 6 lunule contents vary widely. The classification has been based on voltinism, and JARVIS, its author, was unfortunate in that he never saw any specimens from either the Peak district or the Yorkshire Wolds. There are none from either locality in his collection which is housed at the Natural History Museum in London. The differing conclusions via voltinism and lunulation are specific. In the excellent summer of 1995 there were significant second broods of *Aricia* at both Coombs Dale in the Peak district and at Fordon in the Yorkshire Wolds: according to the present view this should not have occurred.

A different situation exists with the colony at Sandhammaren which is bivoltine and where both *allous* and *agestis* are said to co-exist (HØEGH-GULDBERG 1966). This co-existence may be applied erroneously to other sites. In spite of collaboration between HØEGH-GULDBERG and JARVIS there is a difference in approach between Britain and Scandinavia as far as nomenclature is concerned. In north England there is so-called "subspecies" *salmacis* covering the whole area, while in Scandinavia HØEGH-GULDBERG suggested several local "subspecies" to cater for local differences. Typical of these is *Aricia allous rambringi* (HØEGH-GULDBERG, 1966) named after Helge RAMBRING who had first identified the peculiarities of the bivoltine colony at Sandhammaren. Let us suppose that *allous* and *agestis* do exist at Sandhammaren. Because there is a significant data bank which quantifies the male percentage of 5 and 6 lunules on the one hand and of 0 lunules on the other, it is possible to check the status of colonies both at Durham coast and Sandhammaren mathematically. A third useful addition arises from one of JARVIS' cross-pairing experiments. A male *agestis* was paired with a female *vandalica* (JARVIS 1966). From the resulting F1 butterflies a male and a female were paired, and finally 17 males and 4 females of the F2 generation were reared. Of the 17 males 3 showed *agestis* lunulation, 5 showed *allous* and the remaining 9 were intermediates. These figures are incidentally quite close to the 25 % white, 50 % pink,

25 % red in MENDEL's experiment. From data quoted above 82.9 % of *agestis* males have either 5 or 6 lunules. Similarly 57.8 % of *allous* or *artaxerxes* males have 0 lunule specimens. Table 5 below can now be constructed using percentages from Table 3 and the JARVIS data.

Table 5: Checks for hybrids or co-existing "subspecies".

Colony	5 & 6 lunules	% *agestis*	0 lunules	% *allous/artax.*	Total
JARVIS F2	17.6 ± 0.829	21.2	29.4 ± 0.578	50.9	72.1
Durham	8.7 ± 0.829	10.5	32.6 ± 0.578	56.4	66.9
Sandhammaren	25.8 ± 0.829	31.1	14.5 ± 0.578	25.1	56.2

The small correction which might be applied to accommodate 3.1 % of the 5 and 6 lunule portions by using the lower divisor will be less than 0.5 % and can be ignored. None of the totals is anywhere near 100 % and the known cross-breeding check has come out with the highest figure. The conclusion has to be that separate subspecies do not fly together and that hybrids are involved. In connection with the Durham coastal colonies, recent genetic checks via electrophoresis have shown (Janet CAMERON, pers. comm. 1996) that the race there has components of both *agestis* and *artaxerxes* although she has not been able to decide whether a "subspecies" or hybrids are involved. For reasons already stated hybrids are the preferred explanation, a point already made some years ago (FORD 1945). Here it should be mentioned that it is possible to find most points of view supported somewhere in the general literature.

Interpenetration

A strong case can be made for interpenetration and it comes from several different aspects, which are best listed numerically for ease of reference.

1. The Scottish race *artaxerxes* has one major characteristic of white upper forewing discal spots. Occasionally these are also found on the upper hindwings. These spots consist of white scales which give an overall white appearance without magnification, but which consist of varying numbers of dark scales among the predominantly white ones when viewed at say ×20 (SMYLLIE 1992 a). K. G. SCHURIAN (pers. comm.) carried out an experiment on 3 Rügen larvae by placing them in a domestic refrigerator when full grown so that they were exposed to a cool temperature through the critical early pupal stage. Subsequently two

females showed a broad white *albiannulata* ring round the discal spot, while the single male had a white patch on either side of it. In all 3 cases the white scales were much more evident than in the normal specimens. There is little doubt that Scottish *artaxerxes* was formed from *allous* by exposure to a critical temperature in the early stage of pupation: whether this was one exposure or several over the years is a matter of conjecture.

The white scales are readily visible, and therefore are a very good indicator of an *artaxerxes* presence. In Scotland they approximate to 100 % of the discal spot in all specimens. On the Durham coast specimens with white discal spots occur in about 5 % of the population, and as has already been mentioned, genetic tests have established components from both *artaxerxes* and *agestis*. On the south coast of England specimens with varying numbers of scales occur in 1 male in 3 and 2 in 3 females. In central and south England, also in south Sweden very occasional "whitespots" occur (HIGGINS & RILEY 1970). The Rügen colony showed white scales in 1 male out of 24 and 7 females in 21. The variation at any one site can be from no scales up to a whitespot with intermediate numbers from 1 scale upwards. This is what would be expected from MENDEL's laws, and also it shows a decreasing *artaxerxes* presence as the distance from Scotland increases. The distance from the Scottish coast to Rügen is significant at over 1000 km. A colony in Brittany, north-west France, and the colony at Mainzer Sand showed no white discal scales. It seems reasonable to assume that the formation of the Channel halted the southward progress of *artaxerxes* into France, as the Scottish border is only 500 km from the south coast of England. The German situation will be discussed later.

2. Univoltine forms have been noted in the *agestis* colony at Royston (JARVIS 1966), well inside its bivoltine area and 60 km north of central London. This complements the presence of *artaxerxes* white discal scales but also, since the climate is quite good enough for bivoltine emergence, it indicates that *artaxerxes* is obligate univoltine. So climate will not affect *allous* or *artaxerxes,* but it can affect *agestis,* and it will also affect *agestis*-rich hybrids
3. A further pointer comes from the fact that although *agestis* males are relatively well lunulated, they still have 17.1 % of specimens having less than 5 or 6 lunules, and they do have the very occasional specimen

with 0 lunules: 1 in 850 males, also 1 in 512 females. Final proportions would need higher figures.

4. The male Mainzer Sand specimens have similar 5 and 6 lunule characteristics to English *agestis*. The difference is that there are no white discal scales and therefore no *artaxerxes* component. This means that the similar degree of northern penetration has come from *allous*. Numbers are not high enough to be statistically significant, but bearing in mind that general European data conforms, and the large English data bank, the assumption is fair. Since *allous* and *artaxerxes* are essentially similar, it is to be expected that their parallel situations will be similar.

5. The northern boundary of *cramera* can be said to coincide with the north of the Iberian peninsula. A major characteristic of *cramera* is the larger size of lunules on both wings compared with *agestis*. If there is a northward penetration of *cramera*, this should occur as extra large lunules in females which are better lunulated. Occasionally "overlunulated" specimens are found in *agestis* colonies, and a comment about a Durham coast female (JARVIS 1969: "with marginal lunules that would make an *agestis* envious") indicates some *cramera* penetration as far north as Durham. There is also the possibility of a reverse situation. Colour photographs of *cramera* larvae (SCHURIAN 1995) show significant colour variation from a largely green form to one which has rich purple-red dorsal and subspiracular lines. These variations occur in Durham although the colouring is not so intense, and JARVIS has noted this variation in some of his cross-breeding experiments. The distance from the north of the Iberian peninsula to Durham is over 1300 km.

6. Phased emergence is a phrase used to indicate the fact that lunulation decreases during an *Aricia* flight period. Weekly checks established this in 1992 for the univoltine colony at Coombs Dale in the Peak district (SMYLLIE 1992 b), and figures for Sandhammaren in 1951 show this clearly (HØEGH-GULDBERG 1966) through to the second brood. In both cases the reduction in lunulation is a definite trend, but not entirely smooth. A further example via cross-breeding is described in detail by JARVIS (1966). A back-cross between *salmacis/agestis* males and *agestis* females produced adults from 3. VII. 1968. Two inter-se pairings were noted on July 10th and 60 larvae were reared in normal daylight and temperature. The larvae showed variable growth leading to emergence between 24th and 26th August from larvae which resembled *agestis*. There was slower growth in other larvae leading to diapause in varying

instars. The slower rates of growth came from larvae with increasing *salmacis* features. While diapause may be controlled by photoperiod as JARVIS expected, there is reason to doubt that this is the only mechanism involved. For example the *agestis*-rich portion of the larvae developed more quickly than the *salmacis*-rich irrespective of photoperiod. If *agestis* has variable voltinism depending on climate, while *salmacis* (which is known to contain univoltine *artaxerxes*) has contributed to the cross-breeding, then the intermediates will have varying tendencies towards being univoltine and this is bound to have a bearing on their rate of growth. Whatever the precise mechanism, larvae hibernated in several instars which would lead to phased emergence in 1969. Phased emergence has also been noted at a bivoltine *agestis* colony.

7. Just as penetration by *artaxerxes* is indicated by white discal scales, so penetration by *agestis* is shown by an increase in lunulation. Examination of Table 2 shows that no Scottish colony has males or the combination of males and females which are as poorly lunulated as those further north in Norway and Sweden. The *agestis* progress may have been halted by the sea, but it has travelled from Pickering where its lunulation characteristics first change, to the north coast of Scotland, over 500 km.
8. The combined effect of 1. and 7. shows some interpenetration over the whole of Britain. There is similar interpenetration further east between *agestis* and *allous*. The presence of *artaxerxes* at least as far as Rügen has been noted in 1. It is therefore very likely that *allous* has penetrated significantly into Britain. Because this "subspecies" has no white discal scales and poor lunulation it is difficult to identify.

Discussion

This will be concentrated on three main areas; further implications arising from interpenetration, comments on possible mechanisms which could account for colonies with very different lunulation characteristics existing quite near one another, and lastly some brief remarks on where the subgenus *Aricia* may stand in relation to other butterflies.

Further implications from interpenetration

The distances involved, even as low as 500 km, are significant. For a sedentary *Aricia* butterfly this represents many years of dispersal. Although

initial contact must have been between different "subspecies", they will first have had to migrate to any interface zone. Although much information from cross-breeding is valid, tricks have been played with nature in that specimens from hundreds of kilometres apart have been put together. Some of the results and conclusions, particularly regarding genetic imbalance between *agestis* and *artaxerxes* which might well lead to extinction (JARVIS 1969) may have put too great an emphasis on information from cross-breeding between individuals which could not have possibly been achieved naturally. The fact of interpenetration at various levels today is at odds with the indication of genetic imbalance and probable extinction at some time in the past.

It is well known from many cross-breeding experiments that some of the major characteristics of *Aricia* are not consistent at different stages of development. Thus a larva with little or no red coloration may produce a well-lunulated butterfly and vice-versa. When two butterflies mate their progeny have apparently random combinations of characteristics, and one way in which this shows up is that the general trend of decreasing lunulation through the flight period is not always smooth. The genetic bank of a colony is represented by the fertile eggs from various parents, and these will provide the next generation. A description of any one characteristic is provided by the total number of individuals in the colony. When data on any characteristic is built up for a colony the overall picture is bound to approximate more and more closely to the genetic bank. It is for this reason that the lunulation data is meaningful and not an exercise which will give spurious results. It provides an overall view and avoids the pitfalls of making judgements from one particular specimen.

Strictly speaking, a case could be made out for all butterflies in the subgenus *Aricia* being hybrids. This is not to argue against *cramera, agestis, artaxerxes* and *allous* being considered valid subspecies. The first two in particular seem able to accommodate small but definite quantities of other "subspecies" without major lunulation characteristics being affected. The case for *artaxerxes* rests on its characteristic white spots, its lunulation is definitely variable and significant in south Scotland. The precise definition of *allous* in terms of characteristic(s) and therefore its geographical location is not easy – north of Lat. 59° N has been suggested. This leaves the zone between *agestis* and *artaxerxes* in England, and between *agestis* in north Germany and *allous* at Lat. 59° N in Scandinavia with the exception of *vandalica* in north Denmark which is poorly lunulated.

There is little doubt that this zone contains a range of hybrids, and it is interesting to note that hybrids are considered to exist (EBERT & RENNWALD 1991) in south central Germany.

Lunulation variation in colonies near one another

Attention was drawn (SMYLLIE 1992 a) to the most striking difference in England between the coastal Durham colony at Hart Warren with a CC:CP ratio of 0.15, very similar to colonies at Kincardine and Banff in north-east Scotland with a CC:CP ratio of 0.16. The difference between these colonies is that in Scotland, all the butterflies have white discal spots, while Hart Warren conforms to the Durham coast content of approximately 5 % The inland colony at Sherburn hill, only 17 km apart as the crow flies, has an entirely different lunulation characteristic, and apart from Pickering at the point of change, its CC:CP ratio at 1.74 is higher than any other in the hybrid zone. So there is a difference of over 10 times in this small distance. To explain this, it was postulated that differing numbers of *agestis, artaxerxes* and *allous* reached any one site because of restrictions to flight, typically scrub, woodland or water which varied with differing approach directions. This explanation is still a possibility but others which may have contributed are mentioned below. The foodplant at any site may favour one "subspecies". Experiments have shown that females have preferred species for ovipositing when given a choice. An *artaxerxes* female (JARVIS 1966) would only lay on *Helianthemum chamaecistus* (Rockrose) when offered both this plant and *Geranium sanguineum* (Bloody Crane's-bill). Two females resulting from cross-breeding this female with an *agestis* male were offered the same two foodplants in an artificially lit cage. Twice as many eggs were laid on the Rockrose as on Bloody Crane'sbill in a 3-hour period. Also predation via parasites has been found to run at high levels – at least 2 in 3 – in north-west England and south-east Scotland (SHAW 1996). When losses from other predators are added only a relatively low % will survive. In colonies where the southern and northern influences are approximately 50/50 the random nature of predation may work to the advantage of either fraction. Again adverse weather may be critical for certain parts of the whole brood depending on its timing. With phased emergence this may hit one part of the whole brood more than another. The result of any of the above may be to affect the genetic pool and bring about changes which could show as differences in colonies relatively near one another. The position today might depend on any one or a combination of the above. The

variation mentioned above is typical of the whole area even if not as dramatic as the example quoted: it is not possible for this variation to come from any single "subspecies".

The genus *Aricia*

If the eggs of *cramera, agestis, allous* and *artaxerxes* are examined there is no detectable difference at low magnification, say ×10 to ×20. Examination of the eggs of other butterfly species shows that even though there may be general similarity in the eggs of one family, individual species eggs can often be identified by specific differences. This indicates that *Aricia* have come from a common ancestor. Moreover, since they can all cross-breed (the only butterflies in Europe which can?), there must be a doubt as to whether any or all of the forms have progressed to the point where they can be considered separate species, as several investigators maintain. On the basis of eggs, the subgenus *Aricia* is relatively young compared with other species, and has not yet matured. Interpenetration occurs to some extent over the whole area under consideration and is interfering with the longer term drift to separate species. Part of this drift is shown by the very considerable variation in lunulation between *cramera* at the southern end and *allous* at the northern. One conclusion from his observations on *cramera* (SCHURIAN 1995) is that this "subspecies" is *in statu nascendi.* It seems appropriate to extend this phrase to the other "subspecies", and to recognise the broad hybrid zone which has not been appreciably altered by what must be the slower drift to large differences in lunulation. The general situation has to be discussed and interpenetration plus hybrids agreed before appropriate nomenclature can follow.

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